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Measures, perceptions and scaling patterns of aggregated species distributions

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Non-random (aggregated) species distributions arise from habitat heterogeneity and nonlinear biotic processes. A comprehensive understanding of the concept of aggregation, as well as its measurement, is pivotal to our understanding of species distributions and macroecological patterns. Here, using an individual-based model, we analyzed opinions on the concept of aggregation from the public and experts (trained ecologists), in addition to those calculated from a variety of aggregation indices. Three forms of scaling patterns (logarithmic, power-law and lognormal) and four groups of scaling trajectories emerged. The experts showed no significant difference from the public, although with a much lower deviation. The public opinion was partially influenced by the abundance of individuals in the spatial map, which was not found in the experts. With the increase of resolution (decrease of grain), aggregation indices showed a general trend from significantly different to significantly similar to the expert opinion. The over-dispersion index (i.e. the clumping parameter k in the negative binomial distribution) performed, at certain scales, as the closest index to the expert opinion. Examining performance of aggregation measures from different groups of scaling patterns was proposed as a practical way of analyzing spatial structures. The categorization of the scaling patterns of aggregation measures, as well as their over- and in-sensitivity towards spatial structures, thus not only provides a potential solution to the modifiable areal unit problem, but also unveils the interrelationship among the concept, measures and perceptions of aggregated species distributions.

The observation that individuals commonly have non-random, aggregated spatial distributions can be attributed to the very early days of ecology (Fisher 1918, Andrewartha and Birch 1954, Geary 1954, Taylor 1961, Hurlbert 1990, Perry et al. 2002). Describing this pervasive, non-random spatial structure in species distributions remains a fundamental aspect of ecological research (Fortin and Dale 2005). Consequently both synonymous terminology (such as aggregated, over-dispersed, clustered, clumped, autocorrelated, contagious, patchy, etc.), as well as a wide array of aggregation measures that focus on different types of spatial data, have arisen in the past several decades (Dale et al. 2002, Dungan et al. 2002, Perry et al. 2002). Indeed, without a clear understanding of the concept of aggregation and its spatial scaling properties, many of the most interesting and critical problems in ecology cannot be fully addressed. This is because, for instance, intraspecific aggregation patterns are intricately entangled with patterns in species ranges, abundance and diversity (Ives 1991, Shorrocks and Sevenster 1995, Gaston and Blackburn 2000, Wertheim et al. 2000, Gaston et al. 2006). Clarifying the concept of aggregation and documenting how changes in scale influence indices used to describe aggregation (i.e. the scaling pattern of indices), therefore continue to play an important role in unifying theories of macro- and spatial-ecology (Gaston et al. 2006).

A particularly well-recognized characteristic of aggregation measures (indices) is their scale-dependence (where scale refers to sampling grain, or the size of the sampling unit, sensu Dungan et al. 2002). Levin (1992) highlighted the importance of scale effects in understanding ecological processes, and further identified the description of such scaling patterns as an important domain of ecological research (Wiens 1989). In spatial analysis, Openshaw (1984) identified scale dependence as one dimension of the modifiable areal unit problem (MAUP). MAUP is the variation in the nature and pattern of species distributions as a result of ''modifiable'', or changing, sampling and analysis scales (Dungan et al. 2002). Significant effort has been spent on seeking scale-invariant measures in spatial analysis specifically to avoid the MAUP as far as possible (Taylor 1961, Kunin 1998, Harte et al. 1999). This has often been controversial, because the scale-free ideal is much easier to refute than to maintain (Yamamura 1990, Maddux 2004). As a result, Fotheringham (1989) suggested a change in focus in spatial analysis from seeking scale-invariant measures to quantifying rates of change in species distribution measures, i.e. quantifying the scaling relationships of

non-random, aggregated species distributions. This has become the focus of much recent work on quantifying the spatial distribution of species (Plotkin et al. 2002, He and Hubbell 2003, Wiegand and Moloney 2004, Hui et al. 2006, Hui and McGeoch 2008, Hui 2009).

Another complication in spatial analysis is a direct result of the mounting number of aggregation measures developed and used in the literature. Since Fisher (1918) first recommended using spatial variance (i.e. the variance in species abundance across multiple samples), many aggregation indices have been proposed (e.g. see textbooks by Legendre and Legendre 1998, Fortin and Dale 2005). A valuable group of synthetic reviews were published precisely to tackle the classification of spatial heterogeneity (Wiens 2000), mathematical relationships between aggregation measures (Dale et al. 2002), and confusion in the terminology of spatial analysis (Dungan et al. 2002). Nonetheless, it remains a challenge to disentangle the effects of species data, spatial scales, and the choice of aggregation measures on conclusions made about species distributions. Importantly, Hurlbert (1990) warned that every design of a new aggregation index and every modification of a pre-existing aggregation measure inevitably redefines the concept of aggregation, and thus measures only a unique facet of the spatial distribution of a species. Choosing an appropriate measure of aggregation for an ecological study is therefore not a straightforward task, and both the appropriateness of the measure for the purpose at hand, as well as risks of bias and potential misinterpretation associated with this choice must be understood.

Here we simplify this task by clarifying the roles of data, scales, indices and human perceptions of aggregation in the quantification of species distributions. We do so by analyzing a series of spatial point maps generated from an individual-based model to cover a full range of possible structures of species distributions. These maps were then examined across scales using an array of aggregation indices in three categories (i.e. spatially implicit, semi-explicit and explicit) that depend on the degree of spatial information incorporated in the measure (i.e. none, average across space, and point-specific, respectively) (Veldtman 2004). The performance of different aggregation indices at different scales was also compared with perceived levels of aggregation by ecologists and members of the public. This work provides a classification of aggregation measures by scaling pattern and human perception that compliments existing classifications based on conceptual (Wiens 2000, Dungan et al. 2002) and mathematical relationships (Dale et al. 2002).

Methods

Data

We generated a standard plant population dataset from a spatially explicit individual-based model (Supplementary material Appendix 1). Individual-based models have been widely used in the simulation of mixed ecosystems, including models for a wide range of taxa, as well as non-species-specific models (e.g. ATLSS by D. DeAngelis et al. <http://atlss.org/>). An individual in this simulation can be seen as a hermaphroditic perennial plant. The number of n seeds ($n = 10$) is dispersed around the parent, following an exponential distribution $p(x) = \lambda e^{-\lambda x}$ (x is the distance between the seed and the parent; $1/\lambda$ gives the mean distance of seeds to parent, $0.01 \leq \lambda \leq 5.5$) (Jansen et al. 2008) with a randomly chosen direction θ ($0^\circ \leq \theta \leq 360^\circ$). The individuals that produce seeds are randomly chosen with a probability of c ($c = 0.25$) within the population of mature adults (those older than one year). Seeds only germinate if there are no other adult plants within a certain distance d ($d = 0.2$) (as a consequence of resource limitation and overcrowding; HilleRisLambers et al. 2002). In each year, an individual experiences a probability of death (mortality) e ($e = 0.1$). The simulation was performed in a 50×50 unit two-dimensional homogeneous, square area with periodic boundaries (to exclude the edge effect), with a carrying capacity (the maximum number) of individuals being around 20 000 (Hui 2006). This individual-based model is analogous to the forest growth simulators JABOWA, FORET, and SORTIE (Levin et al. 1997), but is distinct from other lattice simulations (cellular automata; Iwasa 2000) because the individuals are not constrained to grids. A total of 33 point patterns (e.g. Fig. 1a) were selected from the simulation based on two criteria. First, the number of points had to be between 0 and 2000 due to the limited capacity of some of the spatial aggregation software (e.g. the maximal number of points that SADIE map ver. 2.0 can handle is 2000). Second, the spatial patterns were chosen to represent close to the full range of possible biologically realistic spatial distributions (Supplementary material Appendix 2 for all 33 point patterns; note that mean ($\pm$standard deviation) abundance in the 33 maps is 803.6 ± 510.1).

Aggregation indices

Thirteen commonly used aggregation indices, belonging to the three spatial heterogeneity categories (Veldtman 2004; i.e. spatially implicit, semi-explicit and explicit; Table 1), were calculated for each of the 33 point patterns for a range of scales (see below). Historically, spatial variance (i.e. the variance of abundance, VoA) was one of the first aggregation measures used to describe the non-randomness of species distributions (Fisher 1918), and was followed by a group of spatially implicit indices based on the variance and mean abundance in samples. For instance, the variance-mean ratio (also called the coefficient of diffusion, CD) (Downing 1991), Morisita's (1962) I_M, Lloyd's (1967) I_L, clumping parameter k in the negative binomial distribution (Bliss and Fisher 1953), and the exponent b in Taylor's power law (TPL; Taylor 1961). Second, with the focus of species distributions shifting from these measures of statistical heterogeneity to spatial structure, spatially semi-explicit (spatial autocorrelation) indices were developed, such as Moran's (1950) I, Join-count statistics (Cliff and Ord 1981) and local density (Iwasa 2000). These spatially semi-explicit indices describe patterned variance (Wiens 2000), and belong to Local Indicators of Spatial Autocorrelation (LISA) statistics (Anselin 1995). More recently, Perry (1995, 1998) developed a spatially explicit index, namely spatial analysis by distance indices (SADIE), based on the distance that would be required to move individuals

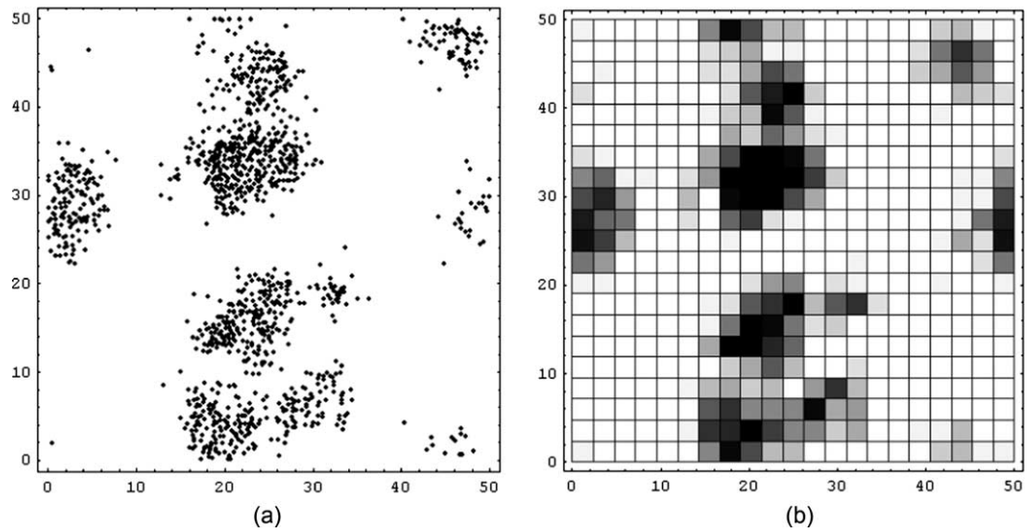

Figure 1. (a) One example of a spatial point-pattern distribution of a species generated by the individual-based model (1167 individuals) and (b) the point pattern distribution of this species converted to grid-based count map of 20×20 units (shading level used here to represent the relative abundance in each patch; black represents highest abundance) (Supplementary material Appendix 2 for all 33 point patterns generated and used in this study).

to achieve a random distribution. This index may be used with point data (SADIE map, Perry 1995) and count data (SADIE shell, Perry 1998), in which SADIE map has been categorized as a spatially semi-explicit index (Veldtman 2004). Besides these indices of spatial statistics, fractal dimension (Mandelbrot 1973) and area-of-occupancy (AOO; Kunin 1998) have also been used to describe the spatial structure of species distributions (Wilson et al. 2004,

Table 1. Spatial statistics used in the analysis of 33 simulated species distributions. Three types of aggregation index include: I = spatially implicit indexes describe variation in a measured variable across a series of samples in a study site without reference to their physical spatial position. SE = spatially semi-explicit indexes describe average spatial dependencies or spatial patterns in a variable measured across an area, although the variation described is not explicitly related to any particular location within the study area. E = spatially explicit indexes describe spatial variation in a measured variable that can be related to a particular location or area within the study site. Scaling forms were determined using the scaling patterns of aggregation (Fig. 2), and the trajectory groups were determined using multi-dimensional scaling (Fig. 3).

Index	Biological interpretation of index	Type	Scaling form	Trajectory group	References
Variance of abundance (VoA, σ^2)	Variation in the number of individuals across samples	I	↑p	I	1
Coefficient of diffusion (CD, σ^2/μ)	Average skew in the number of individuals per sample	I	↑p	III	2
Morisita (I_M) and Lloyd (I_L) indices	Probability that two randomly selected individuals will be from the same quadrat	I	↕n	IV	3, 4
Negative binomial, k	Over-dispersion, i.e. a higher than expected variance	I	↕n[a]	IV	5
Taylor's power law (TPL), b	Tendency for the variance of the frequency distribution to scale with the mean	I	↕n	III	6
SADIE map, I_p	Distance required to distribute counts equally across samples in space	SE	–	–	7
SADIE shell, I_a	Distance required to distribute counts equally across samples in space	E	↓g	III	8
Moran's I_m (first distance class)	Degree to which points in space are correlated	SE	↕n	III	9
Occupancy (P)	Proportion of quadrats with at least one individual	SE	↑[b]	I	
Area-of-occupancy's slope (AOO)	Rate at which the area occupied decreases with increasing linear resolution	SE	↓p[c]	II	10
Box counting fractal dimension, D	Tendency for spatial pattern to repeat across scale	SE	↑p	I	11
Local density (LD)	The conditional probability that a grid cell adjacent to an occupied one is also occupied	SE	↑g	II	12
Joint-count statistics (JCS)	Degree to which local density is larger than global density	SE	↕n	IV	13

Arrows ↑, ↓ and ↕ indicate the values of the index increase, decline and show a unimodal with the increase of grain size, respectively; p: power-law form; g: logarithmic form; n: lognormal form. [a]A transformation, $1+1/k$, was used in calculation; [b]occupancy scaling was not according to any of these three forms but according to a logistic shape (Hui et al. 2006); [c]a transformation, $1/(AOO+1)$, was used in calculation. References: 1, Fisher 1918; 2, Downing 1991; 3, Morisita 1962; 4, Lloyd 1967; 5, Bliss and Fisher 1953; 6, Taylor 1961; 7, Perry 1995; 8, Perry 1998; 9, Moran 1950; 10, Kunin 1998; 11, Mandelbrot 1973; 12, Iwasa 2000; 13, Cliff and Ord 1981.

Hui and McGeoch 2007, Moody-Weis et al. 2008). Although we list only a commonly used subset of published spatial statistics and indices used to measure aggregation, all such measures may be categorized into one of the three spatial heterogeneity categories outlined here (Table 1; see also Veldtman 2004).

The calculation of most indices requires the transformation of point data to count data. We did so by dividing the point map into grid-squares varying from 2×2 to 300×300 units (Fig. 1b; full dataset of the results is in Supplementary material Appendix 3). After subdivision (Fig. 1b), the number of individuals per cell were counted to generate the count data at different scales (grains). For the spatially implicit indices (Table 1), the indices are calculated directly from the count data. The exponent b in Taylor's power law was obtained from log-transformed data of the regression of the variance on mean abundance (Taylor 1961). The b value at $m \times m$ scale indicated the slope of the linear regression curve of the data from $(m/2) \times (m/2)$ to $m \times m$ scales (e.g. the b value reported for the scale of 6×6 units is calculated from the regression of the variance against mean abundances at the scales 3×3, 4×4, 5×5 and 6×6 units). The clumping parameter k in the negative binomial distribution at scale $m \times m$ was calculated from the equation, $1 - P_m = (1 + \mu_m/k)^{-k}$, where P_m is occupancy (the proportion of cells that have at least one individual in it) and μ_m is the mean abundance at the scale $m \times m$. For the spatially semi-explicit approaches such as Moran's I, the first class value was obtained for comparison with the values of other indices (Rodriguez and Delibes 2002). Local density (LD) and the joint-count statistic JCS (=LD/P) were calculated for the von Neumann neighbours (i.e. four nearest neighbours; Hui et al. 2006). For the index I_p from SADIE map (Perry 1995), point coordinates (e.g. Fig. 1a) were input directly into the software (SADIE map); the values of I_a were only calculated at three scales 10×10, 20×20 and 30×30 due to software limitations (SADIE shell; <www.rothamsted.ac.uk/pie/sadie/>). The slope of the area-of-occupancy and fractal dimensions at scale $m \times m$ can also be obtained by the log-transformed regression of occupancy and scale $(m/2) \times (m/2)$ to $m \times m$. For more detailed descriptions of the calculation of each of the indices, please refer to the key and original references in Table 1. The relationships between these aggregation measures and scale, calculated as above, were then tested against specific shapes (e.g. transformed linear and the density function of lognormal distribution) to characterize their scaling patterns. Abundance and occupancy were also included in the analysis because of their significance in ecological research (Andrewartha and Birch 1954), as well as their influence on our perception of aggregation.

Survey

To explore the general, intuitive understanding of the concept of aggregation, as well as to identify which aggregation indices align most closely with this intuitive understanding, we presented the 33 point maps to 10 persons with no tertiary background in the biological or ecological sciences (whom we term "the public") as well as to 10 persons who have been active in ecological research for between 3 and 30 yr (whom we term "experts"). All persons were asked to score each of the 33 point patterns from 1 to 10, with 10 being most aggregated and 1 least aggregated. Both the words "aggregation" and "clustering" were used interchangeably in the instructions. Each person completed the task independently, and returned their results within 3 h (the survey results are shown in Supplementary material Appendix 4).

We ranked the 33 point pattern distribution maps from lowest to highest levels of aggregation based on public and expert ratings, as well as based on the values of each calculated aggregation index. These ranks were used to quantify the relationships between measures in terms of the relative degree of aggregation that they reflected. This was repeated across the range of scales (grain) used for the scale-dependent measures. Non-metric multi-dimensional scaling (MDS) of the ranks was performed using PRIMER (Plymouth Marine Laboratory) and Euclidean distance for the similarity matrix. We then conducted a Monte Carlo test (Gujarati 2006) to calculate levels of agreement between groups of aggregation indices and the intuitive understanding of the concept of aggregation by experts and the public. One hundred random ranks were assigned to the 33 point pattern maps, and the MDS analysis was repeated on this matrix. As a result, a total number of 4950 distances ($=100 \times 99/2$) between any two chosen ranks (d) was calculated to generate a probability distribution of differences between the two randomly chosen ranks, $prob(d)$. The test of whether two ranks were significantly similar or significantly different, was then based on this frequency distribution; that is, the difference between two ranks $\hat{d}$ is significantly similar if $prob(d < \hat{d}) = 5\%$ (only 5% of the 4950 distances is lower than $\hat{d}$) and significantly different if $prob(d < \hat{d}) = 95\%$ (equal to $prob(d > \hat{d}) = 5\%$; only 5% of the 4950 distance is higher than $\hat{d}$).

Results

The relationship between scale and index value differed markedly across indices (Fig. 2). SADIE's I_a ($I_a = -0.61 \ln(a) + 3.15$) and Morisita's I_M (the same is for Lloyd's I_L), as well as the slope of area-of-occupancy AOO (note that a transformation of the slope AOO was used for regression: $1/(\mathrm{AOO}+1) = 0.5a^{0.11}$) declined monotonically with an increase in grain size a (reduction in grid cell number). By contrast, values of the variance of abundance ($\mathrm{VoA} = 1.91a^{1.5}$), occupancy, local density ($\mathrm{LD} = 0.11 \ln(a) + 0.43$), the coefficient of diffusion ($\mathrm{CD} = 4.7a^{0.47}$) and fractal dimension ($\mathrm{D} = 1.45a^{0.06}$) increased (i.e. increasing degree of aggregation) with an increase in grain. Each specific model (in brackets above) provided a good description of the scaling pattern (high goodness-of-fit, $R^2 \geq 0.97$). Four indices were found to have a unimodal, lognormal relationship with scale,

$$Index = \frac{z}{\sigma\sqrt{2\pi}} e^{-\frac{(\ln a - \mu)^2}{2\sigma^2}},$$

with aggregation intensity reaching a peak at intermediate grain sizes (Fig. 2). These four indices were Moran's I ($z = 5.0$, $\mu = 1.17$, $\sigma = 1.91$), the joint-count statistics ($z = 5.6$,

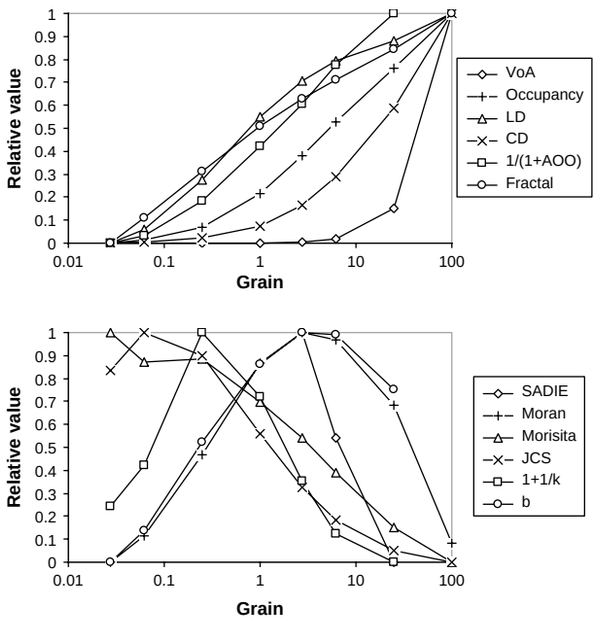

Figure 2. Scaling relationships of the aggregation indices (separated here into negative and unimodal (above) and positive (below) scaling relationships). The value of aggregation indices were transformed to relative values I_R ($I_R = (I_{Real} - I_{MIN})/(I_{MAX} - I_{MIN})$ for comparison, where I_{Real} is the real value of the index, I_{MAX} and I_{MIN} are the maximum and minimum values of the index, respectively). See Table 1 for acronyms.

$\mu = -2.34$, $\sigma = 2.23$), k in the negative binomial (Index = 1 + 1/k, $z = 3.5$, $\mu = -1.06$, $\sigma = 1.4$) and b of Taylor's power law ($z = 5.7$, $\mu = 1.38$, $\sigma = 2.2$). The proportion of variance explained by the lognormal model was extremely high ($R^2 > 0.98$). Furthermore, if we only consider grain sizes with a mean abundance greater than one (that is when the number of grid cells is less than approximately 28×28, i.e. grain is > 3.11 in Fig. 2), all four indices with a unimodal scaling curve decrease with grain. Therefore, when the mean abundance in samples is greater than one, all the indices have a monotonic, either increasing or decreasing, relationship with grain.

The multi-dimensional scaling (MDS) ordination clearly shows that the scaling pattern of the indices follow four trajectories (Fig. 3). In contrast to the above categories of the shape of scaling patterns of aggregation indices (i.e. increasing, declining and unimodal as the logarithmic, power-law and lognormal functions of grain size a; Fig. 2), groups of the four trajectories based on the MDS revealed clear differences in the outcome as a result of using these indices in identifying aggregation at different scales (Fig. 3; Table 1). The first group (I), which includes the fractal dimension, occupancy and the variance of abundance (VoA), converged on the opinion that species with high abundance are highly aggregated with a decrease in grain size (an increase in number of cells in the lattice) (Fig. 3a). The second group (II), including area-of-occupancy (AOO) and local density, converged on the opinion of the public with a decrease in grain size (Fig. 3b). The third group (III), including Moran's I, SADIE shell I_a (note only three scales are presented), the coefficient of diffusion (CD), as well as b-TPL, converged broadly on the opinions of both experts and the public

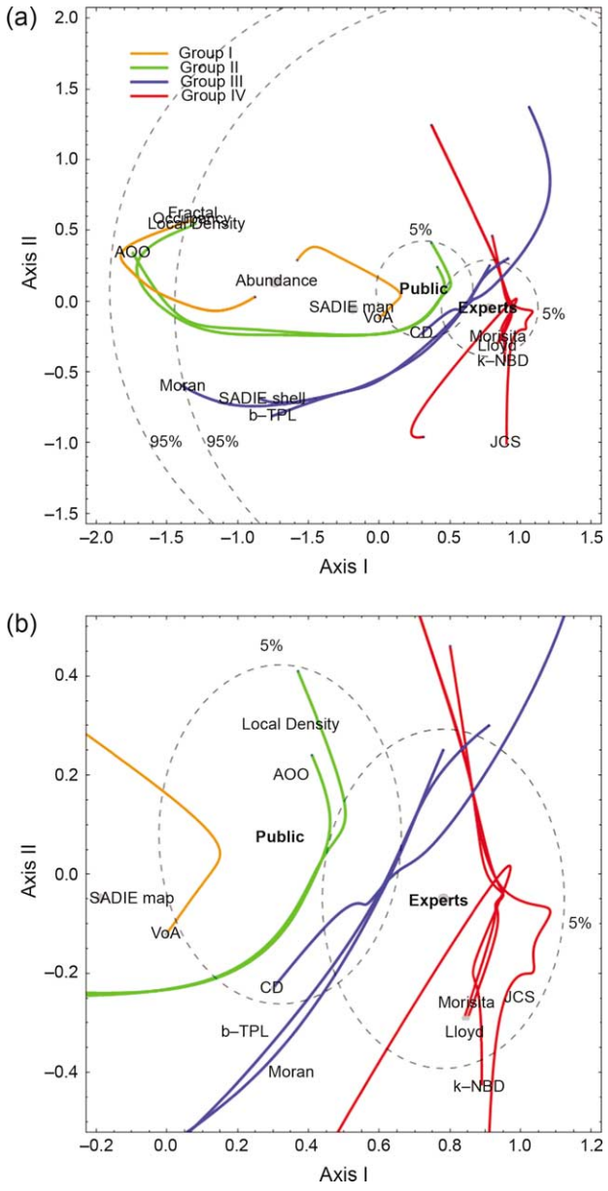

Figure 3. Multidimensional scaling ordinations illustrating the relationships between the aggregation indices (including public and expert assessments, as well as occupancy and abundance) of 33 point patterns across scales. Lines on the ordination connect index positions across scales for the scale-dependent indices, with each scale-dependent index starting from a lattice of 5×5 (coarse grain/scale) and ending at 300×300 (fine grain/scale). Exceptions are b-TPL and AOO that start from 10×10 and k-NBD from 20×20. The index name is positioned at the coarsest scale of its trajectory. Plot (b) is an enlarged section of plot (a). Dashed circles indicate significantly similar (within 5% circle) and different (beyond 95% circle) regions of expert and public assessments, based on a Monte Carlo test. Groups of closely related trajectories (Table 1) are shown in different colours.

(Fig. 3b). The fourth group (IV) agreed with the opinion of the experts at a certain range of scales (from about 10×10 to 100×100), including the joint count statistics (JCS), Morisita's I_M (also Lloyd's I_L) and k-NBD (Fig. 3b).

The Monte Carlo test showed that at a distance less than 0.3423 in MDS, the aggregation measure will be significantly

similar ($p < 0.05$) to that of the experts (the 5% circle in Fig. 3); at a distance > 2.226, the aggregation measure will differ significantly ($p < 0.05$) from expert opinion (the 95% circle in Fig. 3). Five indices (fractal, occupancy, local density, area-of-occupancy and Moran's *I*) were found to be outside the 95% circle for large grains (coarse scale). Eight indices were found within the 5% circle for a particular range of scales (including local density [200 × 200], coefficient of diffusion CD [from 10 × 10 to 100 × 100], Moran's *I* [from 100 × 100 to 300 × 300], *b*-TPL [from 100 × 100 to 200 × 200], *k*-NBD [from 30 × 30 to 100 × 100], Morisita I_M [from 5 × 5 to 100 × 100], Lloyd I_L [from 5 × 5 to 100 × 100] and the joint count statistics JCS [from 10 × 10 to 200 × 200]). With the exception of local density, the other seven indices were also found within the 1% circle (the distance < 0.1825 in MDS, $p < 0.01$) for particular scales, with the minimum distance to expert opinion found for *k*-NBD at the scale of 100 × 100 lattices ($F_{1,31} = 512.4$). Furthermore, coefficient of diffusion (CD), *b*-TPL and Moran's *I* significantly ($p < 0.05$) agree with both opinions of the public and experts at certain scales. SADIE map and shell (I_a) fell between the 5 and 95% circles, i.e. they neither significantly coincide with or differ from public and expert opinion. Considering SADIE shell has the same trajectory as Moran's *I* and *b*-TPL, it should eventually lie within the 5% circle for finer scales (e.g. 100 × 100).

The intuitive understanding of the concept of aggregation by the public (E) was not significantly different from that of experts (P) ($\mu_P \neq \mu_E$, t-value $= -0.146$, DF $= 64$, $p = 0.885$). However, the public's understanding of the concept of aggregation was much more variable than that of the expert group ($SD_P > SD_E$, t-value $= -8.88$, DF $= 64$, $p < 0.001$). Of the 33 simulated distribution maps, only 5 were rated significantly differently by the two groups (Fig. 4). For highly aggregated distribution maps, the public gave the point patterns lower scores than the experts. By contrast, the public scored the moderately to least aggregated point patterns more highly than experts (Fig. 4). The maps that exhibited the greatest discrepancy were those that the experts regarded as least aggregated but the public gave a moderate score (Fig. 4). Moreover, the intuitive understanding of aggregation by the public was positively correlated with abundance (abundance $= 4.09 + 0.0017 \times$ public, $r = 0.534$, $p < 0.01$), while the expert assessment of degree of aggregation was not influenced by abundance (abundance $= 5.09 + 0.0004 \times$ experts, $r = 0.079$, $p = 0.66$).

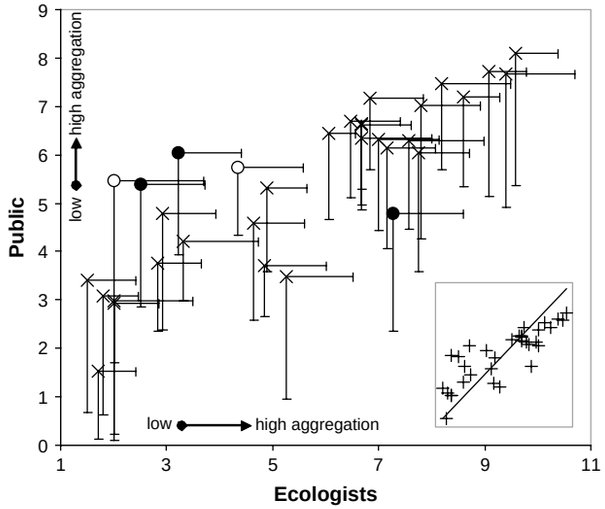

Figure 4. The relationship between the mean assessments of 10 ecologists (i.e. experts) (x error bar indicates the standard deviation) and 10 members of the public (non-biologists) (y error bar indicates the standard deviation) on the aggregation of the 33 point maps (Supplementary material Appendix 2). Paired means shown as not significantly (t-test, see text) different (×) or significantly different (○, $p < 0.05$; ●, $p < 0.01$). The insert shows the general relationship compared to the $y = x$ line.

Discussion

The results of the present study are significant for several reasons. First, while many studies have considered the performance of aggregation indices at different scales (i.e. scaling patterns) (Garcia and Ortiz-Pulido 2004, Davis et al. 2005), as far as we know none have examined the full-range of possible species distributions. We identified three general scaling patterns of the mean value of these aggregation indices for the first time (Fig. 2). Although the scaling patterns of aggregation reported in this study are diverse, the three robust forms emerge (i.e. logarithmic, power-law and lognormal). Second, several studies have classified aggregation indices according to their data requirement, the type of heterogeneity described and their mathematical basis (Wiens 2000, Dale et al. 2002, Dungan et al. 2002), whereas none have classified them according to their scaling patterns (Fig. 2 and 3). For example, Dale et al. (2002) classified aggregation indices by performing an ordination on ten criteria (mostly subjective descriptors, such as data type and gliding criterion). Our ordination has two obvious advantages over previous classifications: 1) we used objective criteria based on the values from aggregation indices, and 2) each index was described by a trajectory across scales, rather than a single value. Finally, the relationship between our intuitive understanding of the concept of aggregation and the outcome of aggregation indices has not previously been examined (discussed below).

Differences in the scale sensitivity of aggregation measures, highlighted in the results, produces inconsistencies within, and non-comparability between, the values of different aggregation measures across scales in spatial analysis (i.e. the modifiable areal unit problem, MAUP) (Openshaw 1984). For example, individuals in map 26 (SADIE shell $I_a = 2.465$) are more aggregated than in map 2 ($I_a = 2.419$) at the scale of 20 × 20 lattices; yet the reverse is true for 30 × 30 lattices (map 26: $I_a = 3.091$; map 2: $I_a = 3.409$). It is, therefore, necessary to caution to what extent (or at which scale) one can rely on assertions that species aggregation increases with abundance (Wilson et al. 2004). Clearly designing more sophisticated, but scale dependent, aggregation measures contributes little to solving the MAUP in spatial analysis. In fact, any scale-dependent values of an aggregation measure reflect two components: species distributional structure as well as the properties of the aggregation measure itself. If species distributional structure is scale-invariant, seeking a scale-free index in spatial analysis will be ideal for solving the MAUP. Some indices such as *b*-TPL and fractal dimension have been

recommended precisely in pursuit of a scale-free index (Taylor 1961, Kunin 1998, Harte et al. 2001), yet here we show that neither one is scale-free (see also Hui and McGeoch 2007). Failing to find such a scale-free index could imply that species distributional structure itself is scale-dependent.

By contrast, Fotheringham (1989) and Jelinski and Wu (1996) called to embrace the MAUP as an opportunity to understand spatial complexity rather than see to it as a hurdle. The three robust scaling forms of aggregation (logarithmic, power and lognormal) that we have identified shed light on the spatial complexity of species distributions, i.e. even though these three scaling forms describe different responses of aggregation indices to changes in scale, they all pinpoint the logarithmic grain as the basic unit for the scaling structure of species distributions. This is because the log-transformed grain can, to a large extent, linearise the effect of spatial scale on species distributional structure, suggesting a semi/quasi-fractal structure of species distributions (Sizling and Storch 2004, Hui and McGeoch 2007, Storch et al. 2008).

Besides the oversensitivity of aggregation indices to spatial scale as portrayed by the MAUP, an issue of insensitivity needs to be emphasized. If two different spatial maps have identical values as measured using an aggregation index, the interpretation can be dichotomous: either the two maps have the same distributional structure, or the aggregation measure in use is insensitive to the difference between two distributional structures. Different distributional structures can produce the same value when using indices such as CD and *k*-NBD (Hurlbert 1990). Indeed, spatially implicit and explicit indices have been shown to be differentially sensitive to recognizing the non-random structure of species distributions (Veldtman and McGeoch 2004). A practical remedy is using a combination of indices covering all three scaling trajectories (groups II, III and IV; Fig. 3). To further ensure that the results from the different indices are consistent with each other, as well as with the professional understanding of the concept (expert opinion), spatially implicit indices should be used in cases of high abundance with a low number of samples, whereas spatially explicit and semi-explicit indices should be used when the sample size is large with low abundance.

Given the over- and in-sensitivity of aggregation measures to certain distributional structures, it is no wonder that a mounting number of indices have been created to suit specific data requirements. Even though categorization and synthesis in spatial analysis can illustrate which distributional characteristic is being measured (Wiens 2000, Dale et al. 2002, Perry et al. 2002), an a priori definition is needed for both identifying the specific distributional structure of interest (Hurlbert 1990) and for index-quality control. The opinion survey served the purpose of providing an a priori definition and the baseline for evaluating the performance of different aggregation measures. The general, instinctive perception of the public can be summarized by the dictionary entry for aggregation: a group of things placed or occurring closely together. Since high abundance reduces the average distance between individuals, public opinion on aggregation was clearly influenced by abundance. In contrast, scientific training does not greatly change the perception of aggregation, but does give the experts a more unanimous opinion. This expert opinion is not only independent of abundance, but also distinguished from Perry's (1995) concept of the SADIE indices: the effort to change the spatial distribution back to a random distribution. Based on those indices found to be significantly similar to expert opinion (at certain scales), expert opinion can be interpreted as the coarse-scale spatial variance (statistical heterogeneity) and fine-scale patterned variance (spatial autocorrelation), following Wiens' (2000) terminology.

In conclusion, an understanding of the aggregated nature of species distributions is profoundly influenced by the data, spatial scale, indices used and perceptions of the concept of aggregation. Even though the scaling patterns of aggregation indices for particular data can be complicated, three fairly consistent forms (i.e. logarithmic, power-law and lognormal) emerge when averaged over the full range of possible data structures. This suggests a quasi-fractal structure to species distributions. The scaling patterns follow four trajectory groups when examined using ordination, in contrast to the traditional category by data type and mathematical relationships discussed to date in the literature. The MAUP can therefore be mitigated by the use of a combination of indices from different trajectory groups (excluding group I). Most indices are closely related to expert opinion within a certain range of scales. Expert opinion is independent of abundance, whereas public impression of aggregation is affected by abundance. The scaling-pattern trajectories identified here, as well as the relationship between professional understanding of the concept of aggregation and the outcome of aggregation measures, may be used as a basis for selecting suitable measures for a particular study, as well as for better understanding species distribution patterns.

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